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SILVER-LEAF DISEASE (II).

IMPERIAL BUREAU OF MYCOLOGY
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BY

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SILVER-LEAF DISEASE (II).

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Introduction.

The present paper is an account of observations and experiments in connexion with Silver-leaf Disease which have been made since the publication of my paper on the same subject in the *Journal of Agricultural Science* for 1911. I am indebted to the Board of Agriculture for giving a grant to assist this work and to the Cambridge University School of Agriculture for placing at my disposal a plot of land on its farm for most of the fruit trees used in the experiments. I have also to thank Mr R. I. Lynch, Curator of the Botanic Gardens, Cambridge, for providing accommodation for other trees.

In a previous paper [2] on this disease further evidence was given of the ability of the fungus, *Stereum purpureum*, to induce the phenomenon of Silver-leaf and upon it the chief responsibility was laid for the losses caused by the malady in the fruit-growing districts of this country. In that paper (p. 141) I pointed out it would be rash to say that *Stereum purpureum* was the *only* cause of Silver-leaf. Recent investigations have strengthened this view, for specimens of silvered foliage have been seen which I am unable to attribute to the action of *Stereum purpureum*.

Subsequent remarks may be anticipated by saying that the silvering of foliage is a widespread phenomenon which is probably induced by various means, the chief one of which in the fruit-growing districts of this country being the fungus *Stereum purpureum*.

Since my paper was published in 1911, Mr H. T. Güssow [5] has written an account of the disease as it occurs in Canada. He also emphasises the part which *Stereum purpureum* plays in causing Silver-leaf disease in fruit trees, and in general his observations are in close agreement with my own.

All the silvered leaves I have examined exhibit the following features:—The upper epidermis is more or less loose from the palisade cells. There is a marked tendency for the mesophyll cells to fall asunder when sections of the leaf are cut, and so pronounced is this, that it is sometimes impossible to obtain sections of silvered leaves which will hold together. Cavities in walls of epidermal cells as described by Percival[8] are sometimes present but I agree with Güssow that they are not invariably found in silvered leaves. The phenomenon of silvering is primarily due to the accumulation of air either below the epidermal cells or in the cavities of their walls, the presence of air in these places interfering with the normal reflection of light from the surface of the leaf.

Field Observations.

The following supplementary account of the distribution of Silver-leaf should be read in connection with my earlier paper. As indicated there, it has been an almost constant experience to find fructifications of *Stereum purpureum* growing on dead branches of Plum trees which bear silvered foliage on other, living, branches. A photograph of such a tree is shewn in Fig. 1, Plate XII. As the death of such trees proceeds, *Stereum purpureum* develops in increasing abundance both on the branches and on the trunk. On one occasion the fructifications of *Polyporus adustus* as well as of *Stereum purpureum* were found to be growing from the trunk of a silvered Plum tree and *Fomes igniarius* has been seen growing in company with *Stereum purpureum* on several silvered Plum trees, but there is as yet no reason for thinking that either *Polyporus adustus* or *Fomes igniarius* is a cause of Silver-leaf. The latter fungus is frequently found on the branches and trunks of Plum trees which bear normal foliage.

In addition to "Victorias" and "Czars," trees of the following varieties of Plums have been seen to be affected with Silver-leaf: Early Rivers, Pond's Seedling, Monarch, Gisborne, Transparent Gage, Purple Gage, and Green Gage, but these varieties are much less susceptible to the disease than are "Victorias" and "Czars." A large number of branches of silvered Plum trees belonging to various varieties and growing in many different fruit gardens have been examined in order to ascertain whether discoloured wood was constantly present in them or in other portions of the tree with which these branches were directly connected. Such discoloured wood has been

found to be invariably associated with the silvered foliage of Plum trees gathered from plantations and this discolouration (cf. Plate XIII, Fig. 4) is strictly comparable with that found in branches artificially inoculated with *Stereum purpureum*. Stained longitudinal sections of such wood shew abundant hyphae in the water-conducting elements which are often partly filled with a gummy substance to which the discolouration is primarily due. The diseased wood is frequently found a considerable distance below the silvered foliage. The amount of discoloured wood as seen in transverse sections varies considerably, a sector of less than 90° being sometimes present, while at other times an area of more than 180° is dark brown in colour. In these cases the zone of discoloured wood sometimes extends from pith to cambium but more often, as in Fig. 4, a narrow band of healthy wood remains in contact with the cambium. Occasionally several discoloured zones are scattered amongst the healthy tissues. Longitudinally the discoloured wood extends a considerable distance and it can frequently be traced back to the larger branches and to the trunk of the tree. The bark of a diseased branch is not affected as soon as the wood, but once it is attacked, the fungus advances in it, as in the wood, more rapidly in a longitudinal than in a lateral direction. Trunks of Plum trees which have been cut down in an advanced stage of disease always contain a large amount of discoloured wood. Fructifications of *Stereum purpureum* frequently develop on the dead bark of one side of a branch or trunk even though the opposite side is still sound.

The distribution of silvered trees in a plantation of Plum trees is usually sporadic unless the plantation is badly neglected, but in a number of cases in which Plum trees have been cut back for various reasons Silver-leaf has developed on almost every tree subjected to this operation. In one such case the larger branches of twenty healthy Plum trees about 20 years of age were cut back during the autumn of 1910 so that only 2 or 3 feet of each of these branches remained. Branches put forth during 1911 were re-grafted in the spring of 1912. None of these grafts grew and when the trees were examined in May 1912 side shoots arising from the branches and trunk and also suckers springing from the root stock were seen to be silvered. Each one of the twenty trees was affected in the same manner. During October, fructifications of *Stereum purpureum* developed in enormous numbers on each of these trees, both on the branches and on the trunk. The large surfaces exposed when the trees were cut back had not been protected in any way and one can readily imagine the facility given to

Stereum purpureum to effect an entrance by this neglect. The fact that fructifications developed at the base of the trunks of certain trees during October 1912 shewed that the fungus had made rapid progress in the tissues.

During the early part of 1912, Mr W. O. Backhouse, late of the John Innes Horticultural Institution, and Mr M. A. Bailey of the same Institution informed me that some seedling Plums which were growing there exhibited the phenomenon of Silver-leaf. Mr Backhouse gave me the following particulars about these seedlings. The seeds were germinated in 2 inches of soil in boxes and the seedlings became silvery at about the time the roots became cramped. When the seedlings were potted they began to recover their normal appearance. The percentage of seedlings which became silvered before being potted varied in different varieties. Thus "Victorias" were affected to an extent of about 50 per cent., "Magnum Bonums" to about 20 per cent., and "Pershores" also to some extent. It is noteworthy that "Czars" grown under the same conditions were entirely unaffected although this variety in fruit plantations is frequently attacked by Silver-leaf disease. The seeds from which these seedlings were derived were obtained from healthy trees. The "Victoria" seedlings which came from "selfed" flowers were more affected with Silver-leaf than those derived from flowers "naturally" pollinated. Some of these seedlings were sent to me and I examined them with the following results: The silvering was strictly comparable with that which occurs in adult trees. The epidermis was partly free from the underlying palisade tissue and on trying to cut sections of the leaf there was a decided tendency for the mesophyll cells to fall asunder one from the other. There was no evidence of fungus attack in either leaf, stem, or root. As already stated, the seedlings began to recover when given more room in which to grow and upon examining them in August, I saw that the recovery of the foliage to its normal appearance was well advanced. I came to the conclusion that in such a case as this the phenomenon of Silver-leaf was not caused by *Stereum purpureum*. Güssow[5] mentions some cases of the appearance of Silver-leaf in seedling plums, and suggests the possibility either that the disease may be perpetuated by means of the seed or that the seedlings may become infected at a very early stage.

For two years in succession Silver-leaf has been reported on Sloe trees (*Prunus spinosa*) in the Isle of Wight. By the kindness of Miss E. Dale I have been able to examine foliage of one of these trees and

the silvering has been found to be strictly comparable with that occurring in cultivated Plum trees.

Although I have seen comparatively few adult Apple trees shewing Silver-leaf I have frequently found scions of regrafted trees that are silvered.

One group of regrafted Apple trees ("Blenheim Orange") which I saw last summer may be described. Fifteen of these trees were cut back three years ago and were regrafted with scions of either the "Grenadier" or "Jubilee" variety. The grafts grew until the spring of 1912 when those on twelve of the trees rapidly died. When these trees were examined in August, 1912, each stock shewed innumerable sporophores of *Stereum purpureum* growing from the bark, and there can be little doubt that this fungus killed the trees (Plate XIII, Fig. 5). The top of one of these trees was sawn off and examined in detail in the laboratory. When split longitudinally the upper part of the stock was seen to be almost completely discoloured, but there was more healthy wood in one of the grafts, thus shewing that it was the stock which had been most severely affected. Hyphae were present in abundance in sections of the discoloured wood. Some portions of the bark of the stock were still healthy and on these no fructifications were found. Grafts of the other three trees were living and were silvered. In longitudinal section the upper part of the stock shewed much less discoloured wood than in the case previously described and the graft was quite sound. Hyphae were found in sections of the discoloured wood of the stock. Such a tree was probably attacked by *Stereum purpureum* but less severely than the trees bearing dead grafts.

Another example of failure of regrafted Apples may be described. In the spring of 1911 four Apple trees ("Cox's Orange Pippin") were regrafted. None of the grafts "took" and by the autumn of the same year *Stereum purpureum* was growing in great abundance on the exposed surfaces of the stock. One of these trees was subsequently cut back to within 9 inches of the ground and the exposed surface covered with clay. At a later date fructifications of *Stereum purpureum* developed even over the clay.

As already mentioned in my previous paper, silvering of Apple grafts is of frequent occurrence even when the scions grow vigorously. All the leaves of such grafts or only a few of them may become silvered. This happens frequently in Cambridgeshire when scions of "Bramley Seedling" are used, but in a large number of these cases the shoots grow out of the malady in the course of time. In one plantation

21 out of 29 Apple trees regrafted with scions of "Bramley Seedling" shewed silvering of the leaves during 1912. It is doubtful whether all such examples of Silver-leaf are due to *Stereum purpureum* for in some which have been examined the amount of discoloured wood in the upper part of the stock is small, the diseased tissues extending only an inch below the exposed surface three years after the stock was cut back. This amount of discolouration is no greater than frequently occurs during the processes of decay that normally affect the exposed extremities of trees which are not protected from the action of micro-organisms.

In a recent conversation Professor Barker of the National Fruit and Cider Institute told me he has seen Apple shoots which have been cut from healthy trees and kept in the air for a short time assume a silvery appearance. This affection which concerned "King of the Pippins" and other varieties of Apples appeared only during the autumn and was irregular in occurrence. I hope to have an opportunity of examining this phenomenon another year. Whether it is Silver-leaf or some other malady allied to it, the affection is evidently not due to the action of *Stereum purpureum*.

While writing of the genus Pyrus I may mention that a branch of a tree of *Pyrus prunifolia* (the Siberian Crab) growing at the Botanic Gardens, Cambridge, was silvered during the summer of 1912.

Several other silvered Gooseberry bushes and Red Currant bushes have been seen since the publication of my previous account; *Stereum purpureum* was growing on dead wood at the base of some of the Red Currant bushes.

A silvered Laburnum tree has been under observation during 1912. At the end of August last, fructifications of *Stereum purpureum* developed in abundance on a dead lateral branch. This tree had been severely pruned in previous years and the wounds thus made doubtless offered facility for the entrance of the fungus.

In February last I saw some plants of the White Dead Nettle (*Lamium album*) the leaves of which were silvered. This affection appeared to be the same in character as Silver-leaf in fruit trees. The upper epidermis was puckered and somewhat shrivelled in places and it could be readily torn away from the underlying mesophyll. It was difficult to obtain section of the silvered leaves on account of the tendency for the mesophyll cells to fall asunder. Other White Dead Nettle plants observed towards the end of March were seen to be silvered, but in this case only the older leaves of the shoots exhibited the phenomenon of silvering. No sign of fungus attack was visible in

these Dead Nettle plants, and the conclusion drawn was that in this case also Silver-leaf could not be attributed to *Stereum purpureum.*

The Habitats and Characters of *Stereum purpureum.*

Considerable attention has been paid to noting the various kinds of plants on which *Stereum purpureum* fructifies in nature. Sporophores of this fungus have been found in England on dead tissues (wood and bark) of the following trees: Plum, Apple, Red Currant, Willow (various species), Poplar (various species), Birch, Beech, Sycamore, and Laburnum, and doubtless this list will be extended with fuller observation. As is the case with many other fungi which also live a similar, partly saprophytic, partly parasitic, existence, fructifications of *Stereum purpureum* are developed only on dead tissues whether the fungus has been living recently as a saprophyte or as a parasite. As will be described later, pieces of sporophore obtained from a dead stump of a Birch tree in the midst of a wood readily induced Silver-leaf in Plum trees.

The closely allied fungus *Stereum hirsutum* is found commonly on dead Oak and Hazel but I have only once seen it on a member of the Plum family. In this case it was growing on a dead part of the trunk of a Damson, the foliage of which was healthy.

As is well known, the fructifications of *Stereum purpureum* are extremely variable in form (Plates XII and XIII, Figs. 1, 2, 3 and 5). Sometimes they are resupinate, and at other times profusely imbricate. On a branch of a Plum tree which is directly horizontally the fructifications are usually confined to the under surface, from which they project only a short distance. When the sporophores develop on the trunk or on a branch which is directed upwards they are usually densely imbricate. When young the sporophores are purplish in colour but they become dingy with age. The sterile surface is hairy when free from the substratum. The fructifications of *Stereum purpureum* may be found at all times of the year. They develop from the vegetative mycelium only after a spell of wet weather and appear in particular abundance after heavy rains during the autumn. The capacity of the sporophores to dry up and spore again under moist conditions has been referred to in the previous paper. According to my experience the spores are $5—7\mu \times 3—4\mu$ in size, these dimensions being rather smaller than those given by Massee[6].

A method of growing the fungus from spores on blocks of Plum wood has already been described[2, 3]. The sporophores referred to there

have constantly lacked the consistency and form of sporophores as they occur in nature. Nevertheless basidia and spores have been frequently observed on these rudimentary sporophores. Miss Wakefield[13] has pointed out the probability of the existence of physiological varieties of *Stereum purpureum* some of which produce sporophores in artificial culture while under the same conditions others give rise only to vegetative mycelium.

Inoculation Experiments.

The results of a considerable number of inoculation experiments have been already reported. Those given below refer chiefly to inoculations which have not been previously described.

(1) *Inoculation Experiments with Plum trees.*

Inoculations with moist pieces of fructifications of *Stereum purpureum* taken from silvered Plum trees have continued to cause Silver-leaf in Victoria and Czar trees almost invariably. One "Czar" inoculated in this manner during 1911 shewed Silver-leaf in the spring of that year but during the summer it became leafless. No leaves were put forth in the spring of 1912 and during the autumn fructifications of *Stereum purpureum* developed in profusion on the main stem, from the level of the soil upwards. It is evident that this tree was killed by *Stereum purpureum*. The only failure to be recorded in connexion with these inoculations of Victoria Plums concerns three young bushes, the main stems of which were inoculated during December 1911. The foliage of the spring of 1912 was normal and no signs of Silver-leaf developed during the summer. Gumming, however, occurred at the places of inoculation. Two other bushes inoculated at the same time and in the same way produced silvered foliage the following spring. It is difficult to account for these failures. It is possible that for some reason not understood the mycelium failed to establish itself in the tissues with sufficient vigour to cause Silver-leaf and the affection may yet appear next spring, for in some other experiments its appearance has been delayed more than a year. The vigour of the sporophores used in these and similar inoculations was always tested by ascertaining whether control pieces would deposit spores under suitable conditions.

As would be anticipated, the silvering exhibited in the spring is usually the more extensive the longer the inoculation has been made.

When an inoculation is made during the autumn the inoculated branch sometimes dies during the winter, so that no leaves are put forth from the buds of this branch; silvering is however shewn by leaves developed on neighbouring branches. Inoculations made after July frequently do not result in silvering of the foliage until the following spring, but one inoculation of a Victoria Plum made during August 1912 caused silvering less than five weeks later. The leaves which became silvered were fully formed before the inoculation was made.

Salmon [11] has suggested the possibility of the existence of different strains or varieties of *Stereum purpureum*, some causing Silver-leaf and others being inactive in this way. The previous experiments of Spencer Pickering [9, 10] and myself [2] shew that there is probably nothing in the nature of specialised parasitism in the biology of this fungus. The mode of life of a wound parasite differs widely from that of an obligate parasite such as a Mildew or a Rust fungus, and there is less likelihood of a particularly specialised mode of nutrition being evolved in the case of a fungus which may live either saprophytically or parasitically than in one which is an obligate parasite. *Stereum purpureum* is, however, such a common saprophytic fungus upon various kinds of woody tissues that it is a matter of importance to ascertain if the fungus taken from tissues where it is not associated with Silver-leaf can produce this phenomenon in Plum trees. The following experiments in this connexion have been performed. Small portions of the sporophores of the fungus obtained from a dead Birch stump in the midst of a wood were placed in 12 branches belonging to two different Victoria plum trees, 4—5 years of age, during October 1911. In April 1912 when some of the buds opened, all of the 12 inoculated branches shewed silvered leaves. Many of the foliage buds of the inoculated branches, however, did not open, and the leaves which did develop, rapidly died so that the inoculated branches became bare. Eight of the inoculated branches were leafless by the end of April and some shoots which had meanwhile developed on the main stem of one tree two and a half feet below the level of the inoculations had become silvered. By the middle of June all the inoculated branches were leafless and the leaves of shoots which were being thrown up by the root stock were silvered. In this connection it is to be noted that all the Plum trees which have become seriously affected with Silver-leaf after inoculation have put forth numerous shoots both from the base of the stem and also from the root stock as though the trees were making strenuous efforts to free themselves from the disease. Fig. 6 is a

photograph of one of these trees taken in the early part of October 1912. It will be noticed that the tree is bare except for the silvered shoots which have developed on one side of the base. At the end of the month fructifications of *Stereum purpureum* began to arise on one side of the trunk of one of these trees throughout its whole length and were especially well developed at soil level on the side opposite that on which the silvered suckers had been thrown up. The tissues of the main stem were dead only on one side and the fructifications arose only from this region. The moist condition of the soil probably accounts for the particularly strong development of fructifications at this level. During the following month *Stereum purpureum* developed in much the same way on the main stem of the other Plum tree inoculated with pieces of sporophore obtained from a Birch stump. It is thus clear that these trees are dying with great rapidity. The trees were perhaps somewhat more severely inoculated than other trees inoculated with *Stereum purpureum* obtained from a silvered Plum tree but, taking this into consideration, they are undoubtedly being more rapidly killed than the latter. These experiments show that *Stereum purpureum* from such a source as a dead Birch stump may be at least as virulent in causing Silver-leaf as *Stereum purpureum* obtained from a silvered fruit tree. Indeed these results engender a suspicion that the fungus may be all the more aggressive for a change of "host."

Additional inoculations with the mycelium of *Stereum purpureum* cultivated in pure culture from spores have been followed by silvering of the foliage in a high percentage of cases. Thus 12 inoculations made in three "Victorias" with this mycelium during December 1911 all resulted in Silver-leaf the following spring. On the other hand 6 inoculations of a "Monarch" and 6 inoculations of an "Early Rivers" made during March 1912 have not hitherto resulted in Silver-leaf. These varieties are not so susceptible to Silver-leaf as the "Victoria" and may possibly resist the disease in these experiments. Two examples of the results of inoculating "Victorias" with the cultivated mycelium will be described in detail.

In one, six branches of a young bush tree were inoculated with cultivated mycelium in December 1911. At the end of April 1912, five of the inoculated branches bore silvered foliage, the other inoculated branch being leafless and apparently dead. Five uninoculated branches also carried silvered leaves. Large masses of gum were extruding both from the places of inoculation and from other points, whereas in control trees of the same variety there was only a trace of gumming. By the

middle of August all the inoculated branches were leafless. On one of the uninoculated branches which shewed silvered leaves in April a "midsummer shoot" had developed but none of its leaves became silvered.

In the other case three branches of a young bush tree were similarly inoculated in December 1911. At the end of April 1912 all the branches, inoculated and uninoculated, shewed silvered leaves and there was profuse gumming at the points of inoculation and at places on the main stem. By the middle of August the general appearance of the bush was about the same, but in this instance some of the leaves at the proximal end of a "midsummer shoot" were silvered.

In the paper of 1911 it was pointed out that of 38 branches of "Czars" and "Victorias" inoculated with the cultivated mycelium 10 became affected with Silver-leaf during that year. During 1912 eight of these inoculated branches were silvered and three of them were branches which did not carry silvered leaves the previous year. Some branches affected during 1911 have evidently recovered.

It was recorded in the same paper that a small number of branches of old Victoria plums inoculated with spores of *Stereum purpureum* had been followed by Silver-leaf. These successful spore inoculations were made during the summer of 1910 and silvering of the foliage resulted in 1911. In these cases spores were inserted into a T-shaped wound immediately after the latter had been made. No such success has followed any of the spore inoculations made in the same way during 1911 in branches of young Victoria trees.

A few weeks ago, another of the branches inoculated with spores during the spring of 1911 but which remained unsilvered during 1912, was cut off in order to trace the progress made by the fungus from the place of inoculation. It was found that a zone of discoloured wood covering about 90 degrees extended from an inch above the wound to $3\frac{1}{2}$ inches below it, the diseased tissues being entirely surrounded by healthy wood. A similar branch cut off 18 months before shewed a zone of discoloured wood extending from three quarters of an inch above to 2 inches below the place of inoculation. It is therefore evident that the fungus has not made rapid progress recently.

On the other hand certain spore inoculations made in older wounds of branches of similar trees have been followed by Silver-leaf. These experiments will be described in detail. They concern two trees, one a "Czar" and the other a "Victoria," each being a half-standard 4—5 years old. In March 1911 six branches of each tree were broken across

so that they were half severed. The wounds thus made were exposed to the action of the weather for three weeks after which two branches of the "Victoria" were cut off above the wounds. At the same time spores of *Stereum purpureum* were inserted in the wounds of the twelve branches. The wounds were then covered with tinfoil and wool and each of the ten partly severed branches was bound in such a manner as to prevent it from being broken off by the wind. None of the inoculated branches shewed Silver-leaf during the summer of 1911 but during the spring and summer of 1912 three inoculated branches of each tree, *i.e.* six inoculated branches in all, carried silvered foliage. In regard to the Czar tree, two branches bore silvered leaves both above and below the places of inoculation; on the other branch only leaves below the wound were affected. Subsequently these three branches together with another inoculated branch which bore only healthy leaves, broke off at the places of inoculation on account of the heavy crop of fruit. In the case of the "Victoria" only one of the inoculated branches showed silvered leaves in April 1912 but two other uninoculated branches closely connected with it also exhibited Silver-leaf. Leaves of another inoculated branch the upper part of which had broken off, became silvered in June and immediately below it an uninoculated branch also carried silvered leaves. Later in the summer leaves of a third inoculated branch, the upper part of which had broken off, became silvered. It may be said here that several branches of other trees kept as controls also became partly severed and hung down during the summer but none of the leaves of these branches shewed Silver-leaf. One of the larger branches of the "Victoria" that carried silvered leaves and to which one of the inoculated branches was attached, was brought into the laboratory during October in order to ascertain what effect the inoculation had had upon the tissues. Passing downwards from the place of inoculation nothing but dead tissue was found until a lateral shoot bearing silvered leaves was reached two inches below, where about half the wood and bark, as seen in cross section, was discoloured in the same way as has been previously described in connection with my other investigations of Silver-leaf disease. Two inches further below, discoloured wood extended over about a quarter of the cross section. Hyphae were present in abundance in longitudinal sections of this zone of diseased wood. The lateral shoot which bore silvered leaves contained no discoloured wood immediately above its junction with the inoculated branch, hence the silvering of its leaves is to be probably attributed to the fungus present

in the diseased wood below. For the following reason as well as for the fact that the wounds were exposed for three weeks before inoculation it is impossible to say with certainty if the mycelium present in the discoloured wood was derived from the spores inserted at the time of inoculation. This wood is in direct continuity with the dead wood immediately below the place of inoculation but, unfortunately, pruning wounds are present on the branch and, as explained below, these prevent one from drawing a more definite conclusion as to the influence of the inoculation. Below an old pruning wound a certain amount of discoloured wood is invariably found, the discolouration being due to the action of various micro-organisms; the dead wood does not usually extend far back but in some cases I have found it two inches below the exposed surface. Hence it is uncertain how much of the tissue has been killed by the influence of pruning wounds and how much by the mycelium derived from the spores used at the time of inoculation. Silver-leaf has not developed in connection with the presence of pruning wounds on any of the other 70 or more young Plum trees used in the investigation and this is a strong argument in favour of the interpretation that the occurrence of Silver-leaf described above, together with the five other cases associated with it, was probably caused by the inoculation of a previously wounded branch with spores of *Stereum purpureum*. This interpretation supports the view that the fungus behaves as a wound-parasite in fruit plantations. Another possible interpretation of these results is that Silver-leaf developed as a consequence of the manner in which the trees were mutilated apart from any influence due to the insertion of the spores. However, Silver-leaf did not appear until the spring of 1912 and had the phenomenon been caused by pathological conditions outside the category of parasitic influences one might have expected it to become manifest during 1911. It is known from previous experiments that the fungus inserted in the form of spores takes considerable time to advance in the tissues sufficiently to cause Silver-leaf, so it is not surprising that the affection did not appear until 1912.

It is of interest to note that none of the control inoculations performed last year with pieces of dead sporophores of *Stereum purpureum* and with pieces of living sporophores of *Stereum hirsutum* and *Polystictus hirsutus* have been followed by Silver-leaf. Inoculations made during the summer of 1912 with *Stereum rugosum*[1] have not yet

[1] I am indebted to Miss Wakefield, of the Herbarium, Royal Botanic Gardens, Kew, for kindly sending me material of *Stereum rugosum*.

resulted in silvering. Two branches of a Czar tree inoculated with *Stereum hirsutum* were investigated in the laboratory in order to see if the fungus had developed in the tissues. I found that it had made considerable progress in each branch. Thus in one branch there was a zone of discoloured wood which extended from four inches below the point of inoculation to two inches above it, the average amount of diseased wood within these limits being about one third of the area of the cross section. Longitudinal sections of the discoloured zone shewed the presence of hyphae. It is thus evident that *Stereum hirsutum* grows with some facility in the tissues of Plum trees but until the present the phenomenon of Silver-leaf has not been associated with this fungus. Gussow [5] has discovered that *Polystictus versicolor* and *Bjerkandera adusta* grow well in living tissues of Apple trees, but their development in them has not yet been followed by silvering of the foliage. Münch [7] also has pointed out that *Schizophyllum commune*, *Stereum rugosum*, *Stereum purpureum*, *Stereum hirsutum* and other fungi cause extensive discolouration of the sapwood of old trees when inserted by inoculation.

It should be noted that even in control experiments in which a scalpel wound is made in a branch and is subsequently covered with tinfoil and wool, a small amount of discoloured wood is subsequently found around the wound. This is doubtless due to the fact that in outdoor experiments of this kind it is impossible to carry them out under conditions which are completely sterile.

Recovery of silvered Plum trees has already been recorded in previous papers by Spencer Pickering [10] and myself [2]. One of the Czar trees which was conspicuously silvered in 1911 in consequence of inoculation with a portion of a sporophore of *Stereum purpureum* shewed only the merest trace of affection during 1912. Two branches belonging to different trees which exhibited Silver-leaf in 1911 after inoculation with cultivated mycelium of *Stereum purpureum* were entirely unaffected during 1912. In this connection mention should be made of the complete recovery during 1912 of a Laburnum which was silvered in 1911 in consequence of inoculation with *Stereum purpureum*. These cases of recovery may be considered to be due to a check in the growth of the fungus, possibly on account of active resistance on the part of the host.

(2) *Inoculation Experiments with Apple trees.*

Numerous inoculations of young Apple trees have been made with different kinds of material of *Stereum purpureum.* Sporophores from silvered Plum trees, cultivated mycelium, and spores, have been placed many times during 1911 and 1912 in branches of the following varieties of Apple trees: "Lane's Prince Albert," "Lord Suffield," and "Stirling Castle," but until the present only one such inoculation has resulted in Silver-leaf. In this particular case a branch of a bush "Lord Suffield" was inoculated in May 1912 with a piece of sporophore obtained from a silvered Victoria Plum tree and silvering of four leaves at the top of this branch, about two feet above the place of inoculation, became apparent in August. Three other branches of the same tree and four branches of another tree of the same variety were similarly inoculated at the same time but the foliage remained normal throughout the summer. It is evident that in these experiments Apple trees of the varieties named have been much less susceptible to Silver-leaf than are Plum trees. These results may be contrasted with those of Gussow[5] who finds that Apple trees in Canada are readily susceptible to Silver-leaf when inoculated with *Stereum purpureum.* Güssow does not mention the names of the varieties of Apple trees used for the purpose of inoculation. They may have been different from those used by me and this may account for the variation in results.

Upon examining inoculated branches the foliage of which has remained unaffected it is seen that the fungus has made some progress in the tissues. Thus a branch of a "Lane's Prince Albert" inoculated in February 1911 shewed in November 1911 a small zone of discoloured wood that extended two inches below the place of inoculation and an inch above it, the amount of affected wood being relatively much less than is usually the case in similar inoculations of Plum trees.

(3) *Inoculation Experiments with other kinds of Fruit Trees.*

A considerable number of young Cherry trees, chiefly of the "Florence" variety, were inoculated with *Stereum purpureum* in various forms during 1910—11 but none of these trees have become affected with Silver-leaf. Profuse gumming invariably followed the inoculations when pieces of natural sporophores from a silvered Plum tree or cultivated mycelium were used. At a later date a large number of the inoculated branches died rapidly but neighbouring branches remained

unaffected. Investigation shewed that fungus mycelium was abundant in the branches killed in this manner. This mycelium probably belonged to *Stereum purpureum* but although it frequently killed the inoculated branches with rapidity it did not pass thence into other branches.

A Gooseberry bush of the variety known as "Whinham's Industry," inoculated during 1911 with pieces of natural sporophore of *Stereum purpureum*, became silvered during 1912.

Observations on the Manner of Infection and Treatment of the Disease.

The evidence brought forward in the present paper supports the view that in causing Silver-leaf disease in fruit plantations, *Stereum purpureum* behaves as a wound parasite, the disease being spread from one tree to another chiefly by means of spores. There is usually no lack of unprotected wounds on fruit trees and if *Stereum purpureum* is allowed to fructify in a plantation of Plum trees it is likely that Silver-leaf disease will become increasingly prevalent there. Even in fruit gardens that are well managed in other respects, fructifications of *Stereum purpureum* are sometimes allowed to develop with impunity. It cannot be too strongly urged that all tissues on which the sporophores of this fungus appear in fruit plantations should be destroyed. Experiments indicate that *Stereum purpureum* taken from material such as a dead Birch stump is equally as effective in causing Silver-leaf as *Stereum purpureum* taken from a silvered Plum tree, hence no quarter should be extended to the fungus in fruit plantations on whatever substratum it may be found.

Where Silver-leaf has appeared in a Plum plantation experience has shewn that benefit is derived by cutting out affected branches, but in order that this operation may be successful, care must be taken to cut back below the region of discoloured wood. Cases of recovery of trees which are slightly silvered are not infrequent but I see no reason to alter the suggestion previously made that Plum trees which are badly silvered and are beginning to die back, should be destroyed. Reference was made in my earlier paper to the danger of making wood piles in fruit plantations. The prevention of such accumulations is one of the first principles of plant sanitation.

The large amount of pruning and thinning out to which fruit trees are necessarily subjected may be indirectly responsible to some extent

for the malady. Even with rapidly growing Plum trees it is exceptional for a callus to grow sufficiently to protect fully the severed end of a branch from micro-organisms possessing dangerous tendencies.

Grease-banding when not properly carried out is, I think, also an influence which favours the development of Silver-leaf disease. Where the grease has been placed directly on the tree or has soaked through the band, one often sees that the bark becomes torn and dead in places. Such broken tissues offer facility for the development of *Stereum purpureum* and I have seen silvered trees on the torn bark of which *Stereum purpureum* was growing in profusion. Both for this reason and for others which are well known to fruit-growers, the grease should not be placed directly on the tree, the bands should be such that the grease cannot penetrate to the bark, and their position should be altered somewhat each autumn so that the same area of bark is not covered in successive years.

No outbreaks of Silver-leaf have been seen in which it was clear that infection had first occurred in the roots. If a tree that is badly silvered is dug up, a white mycelium is usually found attached to the roots but I have not yet seen any evidence of a tendency for it to spread outwards in the soil. This mycelium is readily traced into the discoloured parts of the wood. Of course if the trees were planted so closely that their root systems interlaced there would be abundant opportunity for infection to occur in a subterranean manner.

It has been suggested by fruit-growers that application of Ferrous Sulphate to the roots of silvered Plum trees is a means of cure, but Spencer Pickering [10] tried this method of treatment on a considerable scale at the Woburn Experimental Fruit Farm a few years ago without success.

A writer in the *Gardeners' Chronicle* [1] has recently given details of a similar method of treating silvered trees which he has found successful. The roots of silvered Plum trees were treated during 1910 and 1911 with heavy dressings of Ferrous Sulphate together with either farm-yard or complete artificial manure. In 1912 the trees thus treated shewed great improvement and one was quite cured. Only a small number of trees were treated in this way so that until the method has been tried on a larger scale it is difficult to pronounce an opinion upon it. The writer of the note was certainly hopeful of this method of treatment.

During the last two years I have had the opportunity of observing some experiments on a method of treating silvered Plum trees with

Ferrous Sulphate in a different manner. These experiments have been carried out near Wisbech by Mr E. Neaverson, who has kindly placed the following data at my disposal. Forty-nine silvered Victoria Plum trees about 20 years of age were treated in the following manner during August 1910: a hole was drilled in the trunk of each tree about three feet from the ground, the hole extending in most cases only to the outer part of the wood; about an ounce of Ferrous Sulphate was inserted in each hole which was afterwards closed with a cork bung. Of the forty-nine trees thus plugged, thirty-seven were slightly affected with Silver-leaf and the remainder were badly diseased at the time of treatment. An examination of the trees in August 1912, *i.e.* two years after treatment, shewed that twelve of the thirty-seven trees slightly infected in 1910 had recovered and were free from Silver-leaf, while none of the twelve trees badly diseased in 1910 had recovered. Thus taking all the plugged trees into consideration 25 per cent. of them had recovered while 34 per cent. of those only slightly affected have been restored to health. It is known that trees lightly attacked by Silver-leaf sometimes recover without treatment, hence it is difficult to lay much stress on the above figures, and in this particular garden one of five untreated silvered trees did recover during the period. On the other hand five of the slightly affected trees which were treated became so badly diseased during the summer of 1911 that they were felled in the autumn. Thus the above method of treating silvered Plum trees, even when only slightly attacked, does not at present appear to give much promise of success. The method is an empirical one, but it was obvious that the method should be seriously considered on account of the faith retained in it by fruit-growers. It is likely that one reason for the use of Ferrous Sulphate as a cure for Silver-leaf lies in the fact that the disease is sometimes confounded with Chlorosis, some cases of which are alleviated by applications of Iron compounds. Ferrous Sulphate placed in the trunk of a tree as in the experiments described above would certainly have a poisonous effect on mycelium present in the wood immediately around the place of application, but it is doubtful whether its influence would be extensive[1].

[1] While this paper was passing through the press a note by Miss Baker on a new treatment for Silver-leaf disease appeared in the *Annals of Botany* for January, 1913. Miss Baker applied, both internally and externally, a concentrated aqueous extract of deliquescing fruit bodies of *Coprinus* to a silvered branch of a Victoria Plum and found that two years later this branch became almost entirely free from Silver-leaf and put forth vigorous new growth. In this note reference is made to the effect of the treatment on one tree only, so the results of its application on a large scale will be awaited with interest.

As indicating the rapid way in which Silver-leaf may spread amongst Victoria Plum trees it may be said that in the garden mentioned above, 17 trees out of 75 which were healthy in 1910 have since become affected by the disease. *Stereum purpureum* was present in abundance on silvered trees in this garden.

General Considerations and Conclusions.

It has been shewn that Silver-leaf is a pathological condition of widespread distribution, the chief cause of the malady in the fruit plantations of this country being the fungus *Stereum purpureum*. This view is held also by Percival [8], Spencer Pickering [9, 10], and Güssow [5]. Examples of silvered foliage have, however, come under observation which, in my opinion, cannot be attributed to the action of *Stereum purpureum*. It is unlikely that the silvering of the leaves of seedling Plums and of such a plant as the White Dead Nettle is caused by this fungus. I look upon Silver-leaf as a general pathological phenomenon which may be caused in various ways, although at present only one of these agents, the fungus *Stereum purpureum*, is known with certainty. It appears likely that Silver-leaf may be caused also by physiological disturbances which are not connected with the action of any parasitic organism as has been suggested by Massee [6a]. It will be remembered that *Stereum purpureum* living in a branch of a Victoria Plum tree may produce silvering of the leaves a considerable distance beyond the region attained by the mycelium; such action at a distance may be due to a disturbance in the transpiration current induced by the presence of the fungus below, though until the present I have been unable to confirm Percival's view [8] that the disturbing agent is an oxidase which is secreted by the fungus. Similar disturbances in the transpiration current may possibly arise from causes not associated with the action of parasitic organisms and the same phenomenon of Silver-leaf may thereby be induced. It is by no means unusual in the pathology of plants and animals for the same kind of morbid manifestation to appear as the result of different pathogenic agents, and in considering Silver-leaf a general pathological phenomenon, I look upon it somewhat in the same way as upon such a condition as, for example, hypertrophy which may be induced both by the action of various parasites and by disturbances in metabolism unconnected with the action of micro-organisms.

The views here expressed on Silver-leaf may possibly harmonise the opinions of those who have considered it to be due to *Stereum*

purpureum with the views of those who have placed it in the category of diseases which are not caused by the action of parasitic organisms. Thus Sorauer[12] in writing of the phenomenon known as "Milchglanz" in Germany, which is doubtless identical with Silver-leaf, describes it under the section devoted to non-parasitic diseases in his *Handbuch der Pflanzen-Krankheiten*. Delacroix[4], who speaks of it as "le plomb" in France, also treats of the disease in the same category.

The manifestation of Silver-leaf depends, I think, partly upon leaf-structure. It is well known that certain varieties of fruit-trees exhibit this phenomenon much more than others and cases have been already mentioned in which Silver-leaf has not resulted although *Stereum purpureum* has made considerable progress in the tissues. I have seen Apple and Beech trees which have been killed by *Stereum purpureum* in all probability, but with which the phenomenon of Silver-leaf has not been associated. Thus just as the phenomenon of Silver-leaf cannot always be attributed to *Stereum purpureum*, so the destructive influence of *Stereum purpureum* is not invariably accompanied by this peculiar affection of the leaves.

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EXPLANATION OF PLATES XII AND XIII.

Fig. 1. Upper part of a silvered Victoria Plum tree, one branch of which is dead and bears fructifications of *Stereum purpureum*.

Fig. 2. Fructifications of *Stereum purpureum* on a dead branch of a Victoria Plum tree.

Fig. 3. Lower part of the trunk of a silvered Victoria Plum tree shewing fructifications of *Stereum purpureum* which developed shortly after the upper part of the tree was cut off.

Fig. 4. Cross section of a branch of a silvered Transparent Gage tree shewing diseased and healthy wood. Twice natural size.

Fig. 5. A Blenheim Orange Apple tree that has died after being regrafted with scions of "Grenadier" or "Jubilee." The scions also have died and the stock bears fructifications of *Stereum purpureum*.

Fig. 6. A Victoria Plum tree as seen one year after inoculation with *Stereum purpureum* taken from a Birch stump. The tree is dying rapidly. Fructifications of *Stereum purpureum* have appeared on the main stem of this tree since the photograph was taken.

Fig. 1.

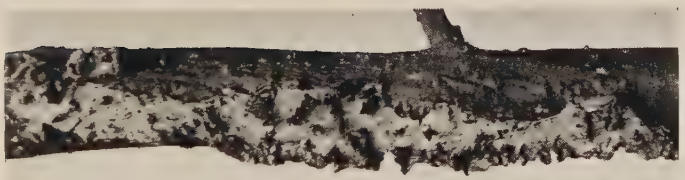

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

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